

SENSITIVITY ANALYSIS OF A GENERAL RANGELAND MODEL

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ABSTRACT

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An extensive sensitivity analysis of a model for the Simulation of Production and Utilization on Rangelands (SPUR) was conducted. A perturb and observe approach was employed in a series of fractional factorial experiments. State variables selected as sensitivity indicator variables included: peak standing crop, maximum plant nitrogen to carbon ratio, integrated year-long mineralization of soil nitrogen, integrated season-long plant death, integrated season-long carbon assimilation, integrated effect of soil moisture on net photosynthesis, integrated season-long forage intake by steers and cumulative season-long change in steer weight.

The 1st of three stages of the analysis showed the dynamics which affect simulated warm and cool-season grasses, warm and cool-season forbs and shrubs were similar in the absence of grazing. Therefore, one plant functional group (warm-season grasses) was used in subsequent stages, allowing a greater number of plant species specific parameters to be examined. In the 2nd stage, also without grazing, optimum, minimum and maximum temperatures for plant activity, the day senescence ends and their joint effects had the largest impacts on the plant component. Characteristics of the soil and soil–water relationships had only minor effects on plant-related indicators. Grazing caused many of the interactions which previously affected plant-related indicators to become less important. Effects associated with day senescence ends were greatly reduced in both magnitude and importance. Steer forage intake and weight change were sensitive to stocking rate and the parameter which converts the percent nitrogen of the forage into total digestible nutrients. Plant parameters which affected the relative quantities of carbon and nitrogen in plant biomass, tended to mediate the effects of livestock-related parameters.

INTRODUCTION

A physically based rangeland simulation model is under development by the Agricultural Research Service of the U.S. Department of Agriculture.

The model, Simulation of Production and Utilization on Rangelands (SPUR), had the following initial objectives:

“To complete a rangeland model that can simulate response of the grassland ecosystem at the Central Plains Experimental Range in north-eastern Colorado in terms of plant standing live and dead biomass by functional groups (cool-season grasses, warm-season forbs, etc.) in g/m^2 , average daily steer weight gain (kg) over a ‘normal’ growing season at a moderate stocking rate, soil moisture content (cm) of the uppermost 45 cm of the soil profile within a ‘normal’ growing season and annual runoff (cm). These variables should be predicted within an interval \pm the coefficient of variation of their field measured values.”

Mathematically, the model is in the form it will have for its initial release to the research community. FORTRAN computer code and complete documentation of the model are available by contacting the second author. In order to identify some of the parameters, driving variables and/or initial conditions which affect achievement of the model objectives and the utility of this model as a research tool, a sensitivity analysis was performed. As this study progressed, it became evident that methodology appropriate for sensitivity analysis of large-scale complex simulation models was not fully developed. Therefore, an approach adopted from Steinhorst et al. (1978) has been extended with some aspects of its interpretation clarified.

Description of the SPUR model

The model consists of components for simulating hydrology, plants and domestic grazing animals. It has sub-components for simulating range wildlife and economics. SPUR is driven primarily by daily maximum and minimum air temperatures, daily precipitation, solar radiation and wind run.

Hydrology component

A modification of the hydrologic model CREAMS (Knisel, 1980) was employed to calculate upland surface runoff volumes, peakflow, snowmelt, upland sediment yield, channel streamflow and sediment. Also calculated is daily soil water balance used to generate soil water tension that control plant growth. Surface runoff is estimated by the Soil Conservation Service curve number procedure (Hanson et al., 1975) and soil loss is computed by the Modified Universal Soil Loss Equation (Williams and Berndt, 1977).

Plant component

At the beginning of a simulation, the state variables for the plant component must be initialized. These include estimates of the biomass in the

standing green, standing dead, live root and propagule compartments, each on a per species basis. Initial values for the state variables of litter, dead roots, soil organic matter and soil inorganic N concentration on a per site basis must also be supplied.

The major portion of the phytomass needed for aboveground development at the start of the growing season comes from the roots. When environmental conditions are right, phytomass is translocated from roots to shoots (TRS). Roots can support only a limited amount of aboveground green biomass, so upward translocation stops when a critical root to shoot ratio is reached. Once upward translocation establishes aboveground green materials, C assimilation begins. Green biomass can be translocated from shoots to roots (TSR) in order to maintain the critical root to shoot ratio.

Once aboveground green biomass is established, photosynthesis and net C assimilation can take place. The maximum photosynthetic rate observed or reported for a plant species is supplied by the model user. This rate is reduced by moisture stress and temperature constraints. Critical points on these response curves are user-supplied. A leaf area conversion factor is used to change biomass to leaf area.

Plant respiration and N uptake, as well as photosynthesis, are in part controlled by a plant activity curve. This curve is composed of a maximum temperature above which no physiological activity can occur, a minimum temperature below which no activity can occur, and an optimal temperature at which activity can occur. Respiration is further controlled by a temperature coefficient, and a maximum dark respiration rate is also user-supplied. Maximum N uptake by roots is a model specification. Root mortality and respiration are controlled by soil water potential and temperature.

Decomposition of dead roots, litter and soil organic matter occurs only if soil inorganic N is present in the system. Maximum decomposition rate is determined as a proportion of the respective pool. The multiplicative effects of temperature and soil water potential subsequently reduce that rate.

Standard enzyme saturation kinetics are used to estimate the N uptake rate. Thus, the theoretical maximum N uptake rate and N use efficiency coefficients control interspecific competition for N. Nitrogen is partitioned in proportion to each species demand if there is not enough inorganic N in the soil to meet the requirements of all species.

The calculation of N transfer from roots to shoots is probably the most critical in the plant model. The flow rate into the shoot directly influences photosynthesis thereby controlling plant growth. Also, this flow controls the N/C for the aboveground plant parts and thus affects forage quality and diets of grazing herbivores. This approach is similar to that of Reuss and Innis (1977).

In general, when C flows from one pool to another, N is sent at a rate

equivalent to the N/C of the donor pool. For example, when cattle trample standing live phytomass, the phytomass going to the litter pool has the same N/C as the standing live biomass. There are, however, several exceptions to the rule. First, when shoots die, the plant 'attempts' to conserve N. Another case occurs in propagule dynamics. There, during seed production, mortality and germination, the N/C is held constant. Finally, leaching is allowed to occur at a constant rate.

Decomposition of dead roots and litter causes a N transfer to the organic pool at the N/C of the respective donor. Dinitrogen (N_2) is fixed as soil inorganic N in proportion to precipitation. Nitrogen is mineralized at a rate necessary to maintain a constant soil organic N/C. Soil water potential and soil inorganic N concentration control denitrification rates. The amount of inorganic N immobilized by the decomposition of litter and dead roots is calculated as the difference between the N needed to maintain the proper N/C in the organic matter and the N released by the decomposition of dead roots and litter. The rates for litter, soil organic matter and dead root decomposition are controlled by a parameter for water potential below which no decomposition can take place.

Herbivores affect the amount of standing green and dead phytomass by consuming the vegetation or by trampling effects of domestic and wild herbivores. All standing live and dead material is available to be trampled, but standing dead is considered to be less resilient than green. Also, herbivory does not explicitly act as a stimulant for plant growth, but if herbivores reduce plant biomass substantially, translocation from roots to shoots can again be initiated. A herbivore model is responsible for returning organic matter and inorganic N to the plant model via excreta. Wind and precipitation also knock down proportions of standing dead. Additional biomass is removed from the aboveground green and placed in the standing dead compartment when ambient temperature drops below a predetermined frost-kill temperature.

Livestock component

The livestock component of SPUR simulates growth and management of stocker cattle under continuous grazing at moderate stocking rates (MacNeil et al., 1985). Dates of turn-on and roundup are exogenous to the model and supplemental energy can be provided for a user specified time period. Subject to any limitation posed by available forage, steers are assumed to graze in accordance with a probability structure that defines preference for location within the pasture and live and dead components of forage functional groups (warm-season grasses, cool-season grasses, forbs, shrubs, etc.). The diet digestibility is inferred from a 2-stage linear function of dietary N

and C. The 1st phase has a positive intercept and slope parameters which relate increases in percent N to increases in digestibility. The 2nd phase defines maximum digestibility and is independent of N and C in the diet. The intake and growth routines have been abstracted from the Texas A&M Beef Simulation Model (Sanders, 1974, 1977; Sanders and Cartwright, 1979) as modified by Notter (1977). Actual intake by steers is determined as the lesser of energy required for satiation and physical capacity, both of which are functions of current weight of the steer and digestibility of the diet. Indigestible dry matter and a fraction of the nitrogen consumed are excreted and returned to the rangeland. Growth of the steers attempts to follow a theoretical growth curve (Brody, 1945) for an average steer in 'good' condition. The asymptotic mature weight parameter, current weight and current age are used to estimate the other parameters required. Condition, or the degree of fatness, varies with the energy level of the diet. When energy from forage is somewhat limited, fat reserves are mobilized to maintain growth of lean tissue and essential fat. If more energy than required to maintain growth of lean tissue and essential fat is consumed, then the excess is stored as additional fat deposits.

MATERIALS AND METHODS

Steinhorst et al. (1978) represented the dynamic model:

$$\dot{X} = f(X, P, D, t) \quad (1)$$

The vector of state variables is denoted as \dot{X} and indicative of differentiation with respect to time, t . The condition of the state variables at any point in time is dependent on the set of functional forms (f) which make up the model and the vectors of parameters (P) and driving variables (D) employed. Sensitivity with respect to f , X , P , and D can be considered and traces of sensitivity through time can be calculated.

Design considerations

Sensitivity analysis of a model can be designed as a series of 2^n fractional factorial experiments (Cochran and Cox, 1957). In fractional factorial experiments, unimportant or insignificant terms of the full factorial design are confounded with those terms thought to be significant or important. In many cases, main effects and lower-order interaction effects are of greater interest than effects of higher-order interactions, thus terms should be confounded accordingly. The number of model runs necessary to discern the importance of lower-order effects is reduced as a result of this confounding. Experimental designs for the fractional factorial experiments are given in the

National Bureau of Standards Applied Mathematics Series (Nat. Bur. Stand., 1957).

The number of parameters, driving variables and initial conditions of interest may necessitate their collection into sets referred to as macroparameters. Macroparameters are usually composed of parameters, driving variables and initial conditions which are thought to have independent and therefore easily discernable effects on the selected sensitivity indicators. The combination of parameters into macroparameters and use of the resultant macroparameters in a fractional factorial experiment follows the logic previously employed by Steinhorst et al. (1978) for the sensitivity analysis of ELM (Innis, 1978).

Sensitivity of perturbed conditions may be expressed as ratios, either:

$$\text{absolute sensitivity} = Z = \sum (S_i - \hat{S}_i) / \sum S_i^2 \quad (2)$$

or

$$\text{relative sensitivity} = R = \sum Z / \left(\sum (\hat{P}_j - P_j)^2 / \sum P_j^2 \right) \quad (3)$$

where S denotes the vector of state variables indexed by i , and P denotes the vector of model parameters and initial conditions indexed by j . Hats over vector representations indicate perturbed vectors as opposed to nominal states.

Multivariate and univariate analysis of variance techniques are then used to analyze the sensitivity ratios. The magnitudes of Hotelling–Lawley traces and mean squares are indicative of the sensitivity of sources of variation in multivariate and univariate analyses, respectively. However, due to the deterministic nature of some models and the class of experimental designs employed, interpretation of resultant F -statistics as tests of significance may not be valid. In fact, for sensitivity indicators completely unaffected by higher-order interactions, the test statistics may be undefined. Hotelling–Lawley traces and mean squares from multivariate and univariate analyses, respectively, might be arrayed from largest to smallest. Sources of variation with associated large mean squares or traces have greater effects on the sensitivity ratios than sources of variation with smaller means squares or traces. To be considered important, the magnitude of a mean square or trace for a sensitivity indicator might arbitrarily be at least 5% of the largest mean square or trace. In addition, effects which have mean squares or traces of the same or lesser order of magnitude than the pooled residual effects are assumed unimportant.

Main effects with major impact on sensitivity ratios do not necessarily imply important differences among conditions of the state variables due to the same source. An alternative is for the state variables to behave as an

interaction of two sources of variation. For this phenomenon to occur perturbation of the indicated effect must have effects which are opposite in sign and essentially equal in magnitude at nominal and perturbed levels of a second effect. The main effect is detected because the sensitivity ratios are derived from distances between levels of state variables without regard to direction. In a manner similar to that discussed for main effects, some 1st-order interactions in the sensitivities may be indicative of 2nd-order interactions.

SPUR sensitivity analysis

At the beginning of the sensitivity analysis, several indicators which reflect the state of the model and the model response to perturbations were identified. These were: the largest amount of standing green material generated on a single day, referred to as peak standing crop, on a species basis; the highest nitrogen (N) to carbon (C) ratio (N/C) for any day of a year, on a species basis; plant death, summed over the year, on a species basis; assimilated carbon per plant species, summed over the year; the summed effect of (soil) moisture on photosynthesis on a species basis (termed EMP; this variable has a value of 1 on days when the plant encounters no moisture stress); mineralized nitrogen summed over the year on a site basis; total weight gain over the grazing season for an average steer; forage intake summed over the grazing season for an average steer; and total runoff for the site over the course of a simulated year.

Unfortunately, the initial release of the SPUR model does not meet the objective of simulation of annual runoff from pastures. Consequently, the sensitivity of simulated annual runoff to perturbation of parameters and initial conditions was not examined.

In all stages of the SPUR sensitivity analysis, each model run began in 1971 on Julian Day 1 (1 January) and ended on Day 365 (31 December) of 1975. Actual weather data from the Central Plains Experimental Range, with the exception of daily wind run, were used. (Wind run was generated using a separate procedure (Haan, 1977)). The sensitivity indicators were measured in the 4th and 5th simulated years to enable the model to adjust for any disequilibrium in initial conditions.

In stage 1, the hypothesis of dynamic similarity of simulated functional groups of forages (warm-season grasses, cool-season grasses, warm-season forbs, cool-season forbs and shrubs) was examined. The sensitivity indicators applicable to functional groups of plant species were measured separately for each of the simulated functional groups. Parameters applicable to each functional group were collected in a single macroparameter rather than being distributed across macroparameters as might be more typical. The maximum

photosynthesis rate, optimum temperature for photosynthesis and temperature for initiation of translocation from roots to shoots applicable to warm-season grasses, cool-season grasses, warm-season forbs, cool-season forbs and shrubs were the component parameters of macroparameters 1.A, 1.B, 1.C, 1.D and 1.E, respectively. These parameters, when perturbed, were altered either plus or minus 25%. Daily maximum and minimum temperatures were an additional component of macroparameter 1.E and a sixth macroparameter (1.F) was composed of daily precipitation and solar radiation. The climatic driving variables were reduced by 30% when perturbed in stage 1. Important 1st-order interaction effects, indicative of dynamic dissimilarity among the functional groups, were of primary interest. Each of the macroparameter main effects was confounded with a 4th-order interaction effect and each 1st-order interaction effect was confounded with a 3rd-order interaction effect. Second-order interaction effects were confounded with other 2nd-order interaction effects and were termed residual effects. Multivariate analysis of variance procedures were used to ascertain the effects of model perturbations on the series of 5×1 vectors of sensitivity indicators when separate measurements were made on each functional group of plant species. Univariate analysis of variance procedures were used to ascertain the effects of model perturbations for indicators that were characteristics of the site and when only one functional group of plant species was included. The analyses were then averaged over years, analogous to whole plot analyses in split-plot statistical models. Time trends in the sensitivities were also examined.

The 2nd stage of the sensitivity analysis was designed to examine the response of the SPUR model without grazing to changes in model parameters, driving variables and initial conditions. Only one functional group of plant species (warm-season grasses) was simulated in stage 2. Therefore, more parameters could be examined than if functional group specific parameters had been included. Macroparameters were formed of supposedly independent parameters, driving variables and initial conditions (Table 1). Main effects were confounded with 3rd and higher-order interaction effects, while 1st-order interactions were confounded with 2nd and higher-order interaction effects. The experiment was designed as a $1/4$ replication of a 2^8 factorial experiment.

After identification of macroparameters which resulted in large alterations of model outcomes when perturbed, an additional experiment was conducted to more definitively identify those parameters, initial conditions and their interactions to which the model was sensitive. This experiment was a $1/128$ replication of a 2^{13} factorial experiment comprised of the parameters contained in macroparameters 2.B, 2.E and 2.H. Some of the 1st-order interactions were of necessity confounded with other 1st-order interactions. How-

TABLE 1
Composition of macroparameters examined in stage 2

2.A	2.B	2.C	2.D
Maximum photosynthesis rate	Plant activity curve parameters	ψ for maximum photo-synthesis	Proportion of biomass for TSR
Wind knock down	Precipitation knock down	Respiration temperature coefficient	Proportion of biomass for TRS
Decomposition ψ^a	Dark respiration	Maximum N uptake rate	Dead root decomposition rate
Initial soil water	ψ for TRS	Initial live roots	Initial litter
		Initial dead roots	Condition 1 curve number
2.E	2.F	2.G	2.H
Root to shoot ratio	Green death proportion	Root respiration rate	TRS temperature
Leaf area conversion	ψ for respiration	Day senescence begins	Organic matter decomposition rate
Frost kill temperature	Root death proportion	Litter decomposition rate	Initial standing dead
Initial inorganic N	Initial organic matter	Root depth	Soil evaporation rate
		Soil porosity	Day senescence ends
		Third bar water potential	
		Soil saturated conductivity	

^a ψ = water potential.

TABLE 2

Composition of macroparameters examined in stage 3

3.A	3.B	3.C
Maximum photosynthesis rate	ψ for translocation from roots to shoots	Plant activity curve parameters
Root depth	N uptake rate by plants	Condition 1 curve number
Maximum and minimum temperatures	Asymptotic steer weight	Digestibility equation slope
Green/dead preference for forage		Age of steers at turnout
3.D	3.E	3.F
Root to shoot ratio	Critical temperature for translocation from roots to shoots	Day senescence ends
Frost kill temperature	Soil evaporation parameter	Precipitation
Steer turnout date	Date to remove steers from pasture	Stocking rate
		Weight of steers at turnout

ever, when a set of confounded 1st-order interactions appeared important, separate 2^2 factorial experiments were conducted to ascertain the importance of each of the confounded two-factor interactions. All effects were confounded with 2nd and higher-order interactions which were assumed to be of negligible importance. Data from both experiments conducted at stage 2 of the sensitivity analysis were analyzed as indicated for the univariate sensitivity indicators in stage one, except that time trends were not examined.

The sensitivity of the SPUR model with grazing by steers was evaluated in a 3rd stage of this analysis. A subset of parameters, driving variables and initial conditions to which the model was either sensitive or insensitive in stage 2 and parameters and initial conditions applicable to the steer growth component were examined (Table 2). The design was similar to the $1/2$ replication of a 2^6 factorial experiment employed in stage 1. In addition to the sensitivity indicators previously used in stages 1 and 2, daily steer weight gain and intake were accumulated over the grazing season in stage 3. The data were again analyzed as indicated for the univariate indicators in stage 1.

RESULTS AND DISCUSSION

The sensitivity analysis conducted on the SPUR model was a test of model response to perturbation of driving variables, parameters and initial conditions. Knowledge of the conditions to which the model is sensitive enables a better understanding of the model itself. Identification of sensitive

(insensitive) parameters also suggests that the corresponding part of the Central Plains Experimental Range grassland ecosystem might also be sensitive (insensitive). However, the expectation of complete conformity between sensitivity analysis results and biological reality is naive; models are merely abstractions of imperfect knowledge. If the represented part of the Central Plains Experimental Range grassland ecosystem is known to be sensitive (insensitive), a similar observation of model sensitivity serves as a qualitative validation of the model. Areas of disagreement indicate important areas on which to concentrate future research and subsequent modification of the model. Most important are the areas where knowledge of the biology of the short-grass prairie ecosystem is not sufficient to assess the observed sensitivity to parameter perturbations. Fruitful future field research efforts lie in these areas.

Dynamic similarity of functional groups of forages (stage 1)

An apparent lack of interaction among macroparameters 1.A, 1.B, 1.C and 1.D in stage 1 indicated similarity in the dynamic response of simulated grasses and forbs to alteration of theoretical maximum photosynthetic rate, optimum temperature for photosynthesis, and temperature for initiation of carbohydrate translocation from roots to shoots. Interactions of macroparameters 1.A through 1.D with macroparameter 1.E were more important than the interactions among macroparameters 1.A through 1.D. The interactions of macroparameters 1.A through 1.D with macroparameter 1.E have two plausible interpretations. First, simulated shrubs, might be dynamically different than simulated grasses and forbs. Alternatively, the dynamic responses of simulated grasses and forbs might depend on minimum and/or maximum temperatures. As all functional groups are modeled with one set of equations in which different parameter sets are employed and no interactions among macroparameter 1.A through 1.D were observed, the latter interpretation seems more plausible. The dynamic similarity of simulated forage species functional groups suggested only one functional group would be required for further stages of the sensitivity analysis. Therefore, stages 2 and 3 were conducted with warm-season grasses as the only simulated plant species. The use of one functional group rather than five enabled the more complete examination of the plant and animal components in these subsequent stages.

The years 1974 and 1975 differed in temperature and precipitation during the growing season with 1974 being relatively warm and wet. Interactions of macroparameters 1.A through 1.E with simulated years and interactions of these macroparameters with macroparameter 1.F containing precipitation and solar radiation parameters were noted for plant related sensitivity

TABLE 3

Stage 2 macroparameters and interactions which exhibited the greatest relative effects on state variables

PSC	PNC	MN	DTH	CA	EMP
2.E (58%)	2.E (50%)	2.E (13%)	2.E (12%)	2.B (64%)	2.E (12%)
2.B (7%)	2.E * 2.H (35%)	2.B * 2.E (12%)	2.B (11%)	2.B * 2.E (5%)	2.E * 2.H (17%)
2.B * 2.E (6%)	2.H (8%)	2.B (11%)	2.B * 2.E (11%)	2.C * 2.D (5%)	2.B (14%)
2.H (5%)	2.B * 2.E (4%)	2.E * 2.F (8%)	2.E * 2.H (8%)	2.B * 2.E (3%)	2.B * 2.E (13%)
2.E * 2.H (4%)		2.B * 2.H (6%)	2.H (6%)	2.B * 2.H (3%)	2.B * 2.H (6%)

State variables are abbreviated: PSC, peak standing crop; PNC, maximum nitrogen to carbon ratio; MN, integrated year-long mineralization of nitrogen; DTH, integrated year-long plant death; CA, integrated year-long carbon assimilation; EMP, integrated year-long effect of soil moistures on net photosynthesis.

Table entries are macroparameter designations (Table 1); in parentheses the percentage of the total variation accounted for by the effect.

TABLE 4

Stage 2 component parameters for macroparameters B, E and H and interactions which exhibited the greatest relative effects on state variables

PSC	PNC	MN	DTH	CA	EMP
A (34%)	E (66%)	A * M (29%)	A (38%)	A (31%)	A (35%)
A * M (28%)	A * E (10%)	A (79%)	A * M (27%)	L (9%)	A * M (29%)
M (19%)		M (19%)	M (19%)	D (6%)	M (23%)
F (2%)				M (5%)	
G (2%)				F (5%)	
				H * L (5%)	

State variables are abbreviated as in Table 3.

Table entries are parameter designations: A, plant activity curve parameters; C, dark respiration rate; D, ψ for translocation from root to shoot (TRS); E, TRS temperature; F, organic matter decomposition rate; G, leaf area conversion; H, root to shoot ratio; J, frost kill temperature; K, initial inorganic N; L, soil evaporation parameter; M, day senescence ends; N, initial standing dead; in parentheses the percentage of total variation accounted for by the effect.

indicators. It appeared the two sets of interactions closely paralleled each other. From the mimicry of interactions with simulated years by interactions with macroparameter 1.F, it was concluded further monitoring of time trends in sensitivity was unnecessary. This also suggested any disequilibrium in initial conditions had been overcome by the 4th simulated year and that differences among simulated years without grazing were largely due to differences in precipitation, temperature and solar radiation.

In-depth testing of the plant component (stage 2)

Stage 2 of the analysis evaluated the responsiveness of the SPUR model without grazing. Macroparameters and interactions which exhibited the greatest relative effects on state variables are presented in Table 3. Macroparameters 2.B, 2.E and 2.H and interactions among them were judged most important to the sensitivity of the model as a whole. In order to verify some of the intuitive evaluation of individual parameters and their interactions, component parameters were examined in a follow-up analysis. The component parameters from macroparameters 2.B, 2.E and 2.H and interactions which had the largest relative effects on state variables are indicated in Table 4. Diagnosis of causal component parameters from macroparameters other than 2.B, 2.E and 2.H is subjective.

Macroparameters 2.B, 2.E and 2.H and interactions of macroparameters 2.B and 2.H with macroparameter 2.E had the greatest affect on simulated peak standing crop. Subsequent analysis of component parameters only partially identified the causal effects. When the plant activity curve parameters were at the nominal level, peak standing crop was very highly sensitive to reduction of the day senescence ends with peak standing crop markedly reduced as a result. When the parameters of the plant activity curve were reduced, peak standing crop was relatively insensitive to the day senescence ends. Additionally, peak standing crop was about equally sensitive to reduction of the organic matter decomposition rate and increases in the leaf area conversion parameter. An interaction of parameters corresponding to the observed interaction of macroparameters 2.B and 2.E was not detected. The inability to detect such an interaction is suggestive of higher-order interactions among the component parameters.

The peak N/C was affected by macroparameters 2.E and 2.H as well as interactions 2.B * 2.E and 2.E * 2.H. The interaction of macroparameters 2.E and 2.H resulted in peak N/C being greatly increased when 2.E was perturbed with 2.H at the nominal level and slightly reduced when 2.H was perturbed. Interaction effects among component parameters corresponding to the observed interactions of macroparameters were relatively minor. The critical temperature to initiate translocation from roots to shoots pre-

dominated the components of macroparameter 2.H and all other parameters. Minor mediation of the effect of the critical temperature to initiate translocation from root to shoot on peak N/C by the plant activity curve parameters was also noted. Maximum N/C was increased when the critical temperature to initiate translocation from roots to shoots was increased and the effect was somewhat greater when the plant activity curve parameters had been reduced.

The sensitivity of year-long integrated soil mineralized N was most affected by macroparameters 2.B and 2.E and the 2.B * 2.E interaction. Lesser effects were noted for interactions 2.B * 2.H and 2.E * 2.F. In terms of model states, the effect of 2.E * 2.F was relatively small. The interaction of the plant activity curve parameters with day senescence ends accounted for much of the variation observed among the macroparameters and their interactions. Mineralization of soil N was increased when the day senescence ends was reduced with the plant activity curve parameters held at their nominal level. However, a small reduction in the mineralization of soil N was noted when the plant activity curve parameters were perturbed.

Perturbation of macroparameters 2.E, 2.B and 2.H affected integrated plant death. The interaction of 2.B with 2.E was of similar magnitude as the effect of 2.B. The 2.E * 2.F and 2.B * 2.H interactions were of lesser magnitude, but also important. Plant death was markedly reduced when macroparameter 2.E was perturbed. However, a similar reduction was not found when component parameters were examined in greater detail. Thus, two explanations for the dramatic effect of macroparameter 2.E remain. Either three or more components of macroparameter 2.E interact to radically alter plant death or one of the components of 2.E interacts with initial standing dead or organic matter decomposition rate. The interaction of day senescence ends and the plant activity curve predominated the supplemental analysis, with the effect of organic matter decomposition rate also being important. Causing senescence to end later, with the plant activity curve at the nominal level, markedly reduced plant death. However, when the plant activity curve parameters were reduced, perturbations of the day senescence ends increased plant death slightly.

In comparison to other indicator variables, carbon assimilation appeared generally less sensitive to perturbation of the macroparameters. Only macroparameter 2.B and the 2.B * 2.E and 2.C * 2.D interactions of macroparameters seemed of major importance. The interaction of macroparameters 2.C and 2.D was manifest as an increase in carbon assimilation when macroparameter 2.C was perturbed with 2.D at the nominal level, but the depression in C assimilation which resulted when 2.D was perturbed alone was not buffered by joint perturbation of 2.C with 2.D. The plant activity curve parameters and the water potential for translocation from roots to shoots

were identified as components of macroparameter 2.B which affected carbon assimilation. In addition, soil evaporation and the day senescence ends in macroparameter 2.H also affected the sensitivity of carbon assimilation. The interaction of water potential for translocation from roots to shoots and initial inorganic nitrogen resulted in carbon assimilation being increased when either was perturbed singly, but reduced when both were simultaneously perturbed. When the soil evaporation parameter was reduced or the day senescence ends increased, carbon assimilation was reduced, the effect of the day senescence ends being 4 times larger than the effect of perturbing the soil evaporation parameter.

The effect of moisture on photosynthesis, EMP, was sensitive to perturbation of macroparameters 2.B and 2.E as well as the interactions 2.B * 2.E, 2.B * 2.H and 2.E * 2.H. When macroparameter 2.E was perturbed with 2.B at the nominal level, EMP was reduced. However, when macroparameter 2.E and 2.B were perturbed jointly, no effect on EMP was noted. Perturbation of macroparameter 2.B increased EMP when macroparameter 2.H was held at both the nominal and perturbed level. The 2.B * 2.H interaction arose because the response to perturbation of 2.B was reduced by over half when 2.H was also perturbed. Perturbation of both macroparameters 2.E and 2.H increased EMP. However, the simultaneous perturbation of both 2.E and 2.H resulted in EMP being increased about one-third less than would be expected if the effects of 2.E and 2.H were additive. When individual parameters were examined, the interaction of plant activity curve parameters with day senescence ends was identified as having a major effect on EMP. Reduction of the plant activity curve parameters with the day senescence ends at the nominal level markedly increased EMP. When the day senescence ends was increased, changes in the plant activity curve parameters had little effect on EMP.

Livestock and the effects of grazing (stage 3)

In stage 3, the response of animal component outputs and the modification of previously observed plant and hydrologic component indicators by grazing were of primary interest. Therefore, comparisons both between nominal and perturbed conditions within stage 3 and comparisons of stage 3 results with those obtained in stage 2 are indicated. Macroparameters and interactions that exhibited the greatest relative effects on state variables are shown in Table 5.

Stage 2 results lead to the expectation that plant activity curve parameters and day senescence ends would interact in stage 3. However, macroparameters 3.C and 3.F did not interact to affect the sensitivity of peak standing crop. Only the effects associated with macroparameters 3.C and 3.E had

TABLE 5
Stage 3 macroparameters and interaction that exhibited the greatest relative effects on state variables

PSC	PNC	MN	DTH	CA	EMP	FI	AW
3.C (51%)	3.C (48%)	3.C (36%)	3.C (36%)	3.C (50%)	3.C (58%)	3.C * 3.E (37%)	3.C * 3.E (21%)
3.E (22%)	3.B (12%)	3.E (14%)	3.E (14%)	3.E (21%)	3.F (13%)	3.C (16%)	3.E * 3.F (15%)
3.C * 3.E (6%)	3.E (11%)	3.C * 3.E (4%)	3.C * 3.E (4%)	3.D (15%)	3.E (5%)	3.E (14%)	3.E (13%)
	3.B * 3.E (11%)	3.C * 3.D (3%)	3.D (3%)	3.D (11%)	3.C * 3.E (8%)	3.B * 3.D (13%)	
		3.B * 3.F (3%)				3.B * 3.E (7%)	
						3.A * 3.C (6%)	

State variables are abbreviated: PSC, peak standing crop; PNC, maximum nitrogen to carbon ratio; MN, integrated year-long mineralization of nitrogen; DTH, integrated year-long plant death; CA, integrated year-long carbon assimilation; EMP, integrated year-long effect of soil moisture or net photosynthesis; FI, integrated season-long forage intake by a steer; and AW, cumulative season-long daily weight change.

Table entries are the macroparameter designations (Table 2); in parentheses the percentage of total variation accounted for by the effect.

substantial effects on peak standing crop. Perturbation of macroparameter 3.C resulted in increased peak standing crop, in agreement with the average effect of reduced plant activity curve parameters observed in stage 2. Peak standing crop had been apparently insensitive to the critical temperature for translocation from root to shoot in stage 2. Since it is doubtful that the date livestock were removed affected peak standing crop, it might be concluded that increased soil evaporation caused the observed reduction in peak standing crop which resulted when macroparameter 3.E was perturbed.

Maximum N/C was sensitive to macroparameters 3.B, 3.C and 3.E and the 3.B * 3.E interaction. No effect associated with macroparameter 3.B or the interaction of 3.B and 3.E was found in the inspection of the state variables. This result suggests a possible higher-order interaction affecting peak N/C. In stage 2, an increase in maximum N/C was observed when the critical temperature for translocation from root to shoot was increased. Here a reduction in peak N/C, presumably due to a reduced critical temperature for translocation from root to shoot, was observed when macroparameter 3.E was perturbed.

Macroparameters 3.C, 3.D and 3.E and the interaction of 3.C with 3.E affected the sensitivity of soil mineralized N. However, the effects on state variables were always less than 4%. Much larger effects had been observed in the absence of grazing.

Integrated season-long plant death was sensitive to perturbation of macroparameters 3.C and 3.E and interactions of 3.B * 3.F, 3.C * 3.D and 3.C * 3.E. However, interaction effects on state variables were small, relative to the main effects. Perturbation of macroparameter 3.E markedly reduced plant death. When macroparameter 3.C was perturbed, plant death increased. A similar response had been noted when the macroparameter which contained the plant activity curve parameters was perturbed in stage 2.

In contrast to stage 2, perturbation of macroparameters in stage 3 had notable effects on integrated season-long C assimilation. Major effects were observed when macroparameters 3.C, 3.D or 3.E were perturbed. When macroparameter 3.C was perturbed, C assimilation was increased, again similar to the increase observed when the plant activity curve parameters were perturbed in stage 2. Perturbation of macroparameter 3.E was manifest as a reduction in C assimilation. Carbon assimilation was reduced when macroparameter 3.D was perturbed.

The main effects associated with macroparameters 3.C, 3.E and 3.F affected EMP as did the 3.C * 3.E interaction. The variable EMP was reduced when macroparameter 3.C was perturbed and increased when 3.E or 3.F was perturbed. The result associated with macroparameter 3.C is difficult to explain in light of stage 2. The apparent effects are opposite of those anticipated if they are assumed to be due to reduction of the plant activity curve parameters.

Integrated intake by steers was sensitive to a variety of main effects and interactions. Variables that had affected forage quantity or quality indicators also affected intake. The main effects of macroparameters 3.C and 3.E had sizeable impacts on simulated integrated season-long intake. Macroparameter 3.C interacted with macroparameters 3.A and 3.E and macroparameter 3.B interacted with macroparameters 3.D and 3.E. The effect of diet digestibility on intake is quite clear in the animal model (MacNeil et al., 1985) and corresponds to the main effect associated with macroparameter 3.C. Previous results would indicate a lower quality forage available in a reduced amount when macroparameter 3.E was perturbed. Thus, a greater proportion of the grazing season would be spent when diet digestibility would be affected by the slope parameter. The interaction of macroparameters 3.C and 3.A is somewhat more bothersome. Macroparameter 3.A had no detected effects on forage quantity (PSC or CA) or quality (PNC). Therefore, it might appear the relative preference for green versus dead plant material would interact with the slope parameter from the increasing phase of the digestibility equation. The reduction of intake when 3.A was perturbed being smaller when 3.C was also perturbed than when 3.C was at the nominal level fits this hypothesis. Explanations of the $3.B * 3.D$ and $3.B * 3.E$ interactions are not readily apparent.

While the system of effects governing intake seemed highly sensitive, the manifestations of intake differences in weight change were somewhat buffered. Interactions of macroparameters 3.C and 3.F with macroparameter 3.E affected cumulative daily weight change. The slope of the increasing phase of the equation to predict total digestible nutrients from C and N and stocking rate were probably the principal components of macroparameters 3.C and 3.F, respectively, which contribute to the observed interactions. When the slope parameter was increased, more highly digestible diets would result and a more rapid increase in steer weight would be expected (Maynard et al., 1979). The mechanism by which the increased diet digestibility effect was mediated by macroparameter 3.E is open to some speculation. However, the indicated mechanism which alters intake could lead to the observed result. Perturbation of macroparameter 3.F led to reduced cumulative season-long weight change. A similar effect would be expected from increased stocking rate (Hart, 1978). The interaction of stocking rate with reduced forage quantity or quality has also been alluded to previously (Hart, 1978).

The apparent insensitivity of cumulative season-long weight change to changes in the length of grazing season is noteworthy. However, steers were turned out early in the year and when they were turned out even earlier, only a low-quality diet was attainable. Removal of steers from pasture was late in the year and as with date of turnout, only a low quality diet would be available. Given the low-quality diet available, steers would be expected to have daily weight change near zero.

The lack of sensitivity of cumulative season-long weight change to green/dead preference for forage was not anticipated. A better system to quantify selectivity of steers among forage parts probably needs to be developed.

CONCLUSIONS

Fractional factorial experiments and the use of macroparameters greatly facilitate tests of a large number of combination of parameters. The necessity of independence among parameters collected into a single macroparameter is of paramount importance. Grouped correctly in a macroparameter, the effects of a change in each component parameter on the indicator variables should be discernable. Fractional factorial experiments involved confounded effects. Which effects are confounded can be controlled. The usual procedure is to confound a single supposedly important effect with several others believed to be unimportant. However, in complex analyses, less than optimum designs may be unavoidable if the number of computer runs is limited.

Taken as a whole, the SPUR model does not seem overly 'fragile'. Perhaps it is not even as 'fragile' as the ecosystem it simulates. The plant and hydrology components seem too independent. Greater sensitivity of plant growth indicators to parameters which influence soil water dynamics was anticipated. With the model in its present form, plant activity curve parameters for each functional group of plant species should be known with a reasonable degree of accuracy. The Julian day on which senescence is to end may also be important in the simulation of plant growth depending on grazing intensity. The plant and animal components interact with the parameters employed in one, ultimately affecting the other. Plant nitrogen dynamics and steer intake and growth respond to the critical temperature for translocation from root to shoot. Parameters which convert percent nitrogen to diet energy density must also be known accurately to simulate livestock performance and control recycling of nitrogen.

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